PROC. BIOL. SOC. WASH.
101(4), 1988, pp. 784–793

TAXONOMIC REVISION OF THE *PHALLODRILUS RECTISETOSUS* COMPLEX (OLIGOCHAETA: TUBIFICIDAE)

Christer Erséus

Abstract.—A complex of small marine tubificids previously regarded as one variable species is revised, partly on the basis of new material from Belize, Barbados, Florida, Hawaii, Great Barrier Reef (Australia), Fiji and Aldabra atoll (Indian Ocean). Four different species are recognized: *Phallodrilus rectisetosus* Erséus, 1979, s.s., *P. deminutius* Erséus, 1979, *P. molestus,* new species, and *P. heronensis* Erséus, 1981. They are distinguished from each other by differences in the number of (both somatic and penial) setae and in the morphology of the spermathecae. All four species exhibit wide geographical distribution in the warmer parts of the world; *P. rectisetosus* and *P. molestus,* at least, appear to be circumtropical.

A complex of closely related intertidal and subtidal tubificids, belonging to the marine genus *Phallodrilus* Pierantoni, 1902, was described by Erséus (1979) as a polytypic species, *P. rectisetosus.* The worms were characterized by their (1) small body size, (2) numerous, straight and sharply single-pointed penial setae arranged in tight bundles, (3) small, spindle-shaped atria, each with two compact prostate glands, and (4) pear-shaped, somewhat bipartite spermathecal ampullae. Material from Italy and France was regarded as the nominate subspecies, while specimens from Bermuda and Florida, having fewer setae in the somatic bundles than those from Europe, were assigned to a separate taxon, *P. rectisetosus deminutius* Erséus, 1979. Later, a third subspecies, *P. rectisetosus heronensis* Erséus, 1981, was established for material from Australia's Great Barrier Reef, separated from the other subspecies on dimensional differences in penial setae and atria. Peculiarities in the appearance of its spermathecae were, however, also noted (Erséus 1981: 16).

The distinction between the nominate *P. rectisetosus* and the subspecies *heronensis* appeared difficult to uphold, when somewhat intermediate specimens were found in Saudi Arabia, and it was therefore suggested (Erséus 1985) that the whole group should be regarded as one taxonomic entity (*P. rectisetosus*), until additional material from other parts of the world and non-morphological data become available. It was suspected (op. cit.) that more than one biological species may be involved, but it was found difficult to express the morphological variation observed in a further taxonomic division.

Subsequently, additional material of this complex has become available, and it is the basis for the present study. Firstly, material from Belize in Central America, consisting of two similar but distinguishable forms, led to a re-appraisal of the original material of *P. rectisetosus deminutius.* Upon re-examination the latter proved to contain the same two distinct forms, now concluded to be separate species. Secondly, specimens from Barbados, the Gulf of Mexico, Hawaii, Fiji, Australia, and Aldabra (Indian Ocean)—either collected by the author or received from other sources—further supported the view that more than one species is involved

in the *rectisetosus* complex. The more than 300 individuals thus available (including the old material), could be separated into four groups, the members of each being slightly but consistently different morphologically from those of any other group, even over great geographical distances. The four forms are now regarded as different species, and they are diagnosed in the present paper.

Except when otherwise stated below, the new material was collected by the author while visiting: (1) the Carrie Bow Cay field station on the Barrier Reef off Belize (operated by the Smithsonian Institution) (1985), (2) the Bellairs Research Institute of McGill University in Barbados (1979), (3) the Lizard Island Research Station in the Great Barrier Reef (1982), and (4) the Mana Island Resort in Fiji (1982); or by Mr. D. Davis (University of Hawaii) and the author, during the latter's stay at (5) the Department of Zoology in Honolulu (1987). The live worms were sorted from sieved washings of sand samples, and then fixed in Bouin's fluid.

Material was also received from the Gulf of Mexico (courtesy M. R. Milligan), and the Aldabra Atoll (Seychelles) in the Indian Ocean (K. Fauchald, Smithsonian Institution). The type series and other material of *P. rectisetosus deminutius* were re-examined during a visit to the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

One worm from Fiji was sectioned and stained in Azan. The other specimens were stained in paracarmine and mounted whole in Canada balsam. Types and other reference material have been deposited in the USNM, the Australian Museum in Sydney (AMS), and the British Museum (Natural History) in London (BMNH).

The penial setae (in segment XI) were counted in all available specimens. Often the bundle on one side of the worm did not contain the same number of setae as that of the other side. For the statistics presented below, n thus refers to the total number of bundles studied, i.e., twice the number of specimens.

Systematics

General description of members of the P. rectisetosus *complex.*—Small, somewhat transparent tubificids, only a few mm long. Prostomium typically phallodriline: generally round, set off from peristomium. Clitellum extending over most posterior part of segment X, whole of XI and most of XII. Somatic setae bifid, with upper teeth thinner and often shorter than lower, and with subdental ligament. Bifids few per bundle, anteriorly up to four in *P. rectisetosus* s.s., but only two to three in other species, posteriorly one to two per bundle. Penial setae (ventral setae of XI) straight and short, sharply single-pointed, with tips often somewhat curved. In most species penials generally more than five per bundle (usually about three per bundle in *P. molestus,* n. sp.), arranged very tightly together, parallel or in somewhat fan-shaped formation within bundle. Bundles median to male pores; latter in line with ventral somatic setae in posterior part of XI. Spermathecal pores usually in line with ventral somatic setae anteriorly in X, near intersegmental furrow IX/X.

Pharyngeal glands well developed in IV–VI. Male genitalia (cf. Figs. 1D, 2C, F) paired. Vas deferens longer than atrium, entering apical end of latter. Atrium spindle-shaped, more or less erect, bearing two compact prostate glands, anterior one attached closer to entrance of vas deferens than posterior one. Outer lining of atrium very thin, inner epithelium ciliated and often granulated. Male pore inconspicuous; penis absent. Spermathecae with sperm in loose bundle or random mass.

Key to the Four Species within the Complex

1. Bifid setae fewer per bundle posteriorly than anteriorly (Penial setae generally more than 5 per bundle) 2

- Bifid setae almost invariably 2 per bundle throughout body (Penial setae generally 3–5, only occasionally more than 5 per bundle) ..... *molestus*

2. Spermathecal ampullae pear-shaped, gradually widening towards inner part and thus not clearly set off from duct (Figs. 2C, F), and with sperm in large bundle or mass (Atria at least about 45 μm long) 3
- Spermathecal ampulla small, somewhat spherical, clearly set off from long duct, and with a few loosely arranged spermatozoa (Fig. 3). (Atria at most about 40 μm long) ..... *heronensis*

3. Bifid setae 2–3(4) per bundle anteriorly, 2 per bundle in postclitellar segments ..... *rectisetosus*
- Bifid setae 2 (occasionally 3) per bundle anteriorly, 1 (2) per bundle in postclitellar segments ... *deminutius*

Phallodrilus rectisetosus Erséus, 1979, *sensu stricto* Fig. 1A

Phallodrilus rectisetosus rectisetosus Erséus, 1979:190–191, fig. 6.—Erséus 1981: table I.

Phallodrilus rectisetosus.—Erséus 1985:136–137, figs. 3–4.

Type material.—In Swedish Museum of Natural History (3086–3087): seven specimens from Ischia, Italy (see Erséus 1979).

Other material.—Re-examined: specimens from Italy, France and Saudi Arabia in author's collection (see Erséus 1979, 1985).—New material: USNM 104941, one specimen from Paiko Beach, Maunalua Bay, Oahu, Hawaii, barely subtidal mixed sand (2 Apr 1987).

Diagnosis.—Length 3.2–11.9 mm, 38–63 segments. Bifids 2–3(4) per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae 25–50 μm long, generally about 7–9 per bundle (total range 4–15, $\bar{\chi}$ = 7.9, SD = 1.9, n = 68). Atria 45–90 μm long. Spermathecal ampullae pear-shaped, with sperm in large bundle or mass.

Description of specimen from Hawaii.—Length and segment number unknown (worm not complete). Width at XI 0.23 mm. Bifids 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae (Fig. 1A) 30–35 μm long, 8 per bundle. Atria about 60 μm long. Spermathecae about 75 μm long, with sperm in ampullae.

Variation in number of penial setae per bundle (Fig. 4).—Italy (n = 58): range 4–11, $\bar{\chi}$ = 7.7, SD = 1.4.—France (n = 2): range 4–7, $\bar{\chi}$ = 5.5, but worm not fully mature.—Saudi Arabia (n = 6): range 6–15, $\bar{x}$ = 10.3, SD = 3.3.—Hawaii (n = 2): 8 (both bundles).

Distribution and habitat.—Hawaii (new record), Italy, Atlantic coast of France and Saudi Arabia (Fig. 5). Intertidal and barely subtidal sand.

Phallodrilus deminutius Erséus, 1979 Figs. 2A–C

Phallodrilus rectisetosus deminutius (part) Erséus, 1979:191–192, fig. 7.—Erséus 1981:table I.

Type material re-examined.—USNM 56200–56202, six specimens from Ferry Reach, Bermuda (see Erséus 1979).

Other material re-examined.—USNM 56223, two specimens from Blue Hole area, Bermuda, coll. by M. L. Jones (see Erséus 1979).—Author's collection: 12 specimens from Bermuda (11 from type locality; 1 from Whale Bone Bay, intertidal). Note that several other individuals from Bermuda, previously assigned to "*P. rectisetosus deminutius*" now are identified as *P. molestus,* n. sp., below.

New material.—USNM 104134, one specimen from N of inner end of dock at Carrie Bow Cay, Barrier Reef off Belize, 0.5 m, patch of poorly sorted medium to coarse sand (6 Nov 1985). USNM 104133, 104135, two specimens from N of dock, Carrie Bow Cay, 1 m, fine to medium sand and rubble (10 Nov 1985). USNM 104132, one spec-

imen from Bellairs Reef, St. James, Barbados, 13–14 m, poorly sorted coarse sand (29 Oct 1979).—Author's collection: two specimens from 50 m N of Carrie Bow Cay, 0.7 m, rubble bed with coarse to medium sand beneath (8 and 24 Nov 1985); two specimens from immediately W of N tip of Carrie Bow Cay, 0.5 m, patch of medium sand amongst scattered rocks and *Thalassia* (8 Nov 1985); one specimen from SW of S tip of Carrie Bow Cay, edge of reef, near beginning of *Thalassia* bed, 2 m, poorly sorted sand (12 Nov 1985); and two specimens (coll. H. R. Baker) from near dock of Carrie Bow Cay, 1.5 m, poorly sorted coral sands with algal debris, roots and *Halimeda* flakes (25 Apr 1982).

Diagnosis.—Length 3.4–5.9 mm, 36–44 segments. Bifids 2(3) per bundle anteriorly, 1(2) per bundle in postclitellar segments. Penial setae 30–46 μm long, generally 5–8 per bundle (total range 4–11, $\bar{x}$ = 6.7, SD = 1.5, n = 60). Atria 60–85 μm long. Spermathecal ampullae pear-shaped, with sperm in large bundle or mass.

Description of material from Belize and Barbados.—Length 3.5–5.8 mm, 36–43 segments. Width at XI 0.14–0.27 mm. Bifids (Fig. 2A) 2(3) per bundle in II–VIII, 1 (very occasionally 2) per bundle thereafter, 28–37 μm long, about 2 μm thick. Penial setae (Figs. 2B, C, ps) 35–40 μm long, about 2 μm thick, 4–8 per bundle. Male genitalia shown in Fig. 2C. Vas deferens about 9 μm wide. Atrium 60–85 μm long, 23–35 μm wide. Spermathecae (Fig. 2C, s) 80–145 μm long, consisting of short ducts and pear-shaped, thin-walled ampullae; latter narrower ectally than entally, maximally 35–70 μm wide; sperm as thick bundle or large mass.

Variation in number of penial setae per bundle (Fig. 4).—Bermuda (n = 38): range 4–11, $\bar{x}$ = 7.0, SD = 1.7.—Belize (n = 20): range 4–8, $\bar{x}$ = 6.2, SD = 1.1.—Barbados (n = 2): range 7–8, $\bar{x}$ = 7.5.

Remarks.—The single individual from Fowey Rocks, Miami, Florida, that was identified as "*P. rectisetosus deminutius*" by Erséus (1979) is actually a specimen of *P. molestus*. However, although *P. deminutius* co-occurs with *P. molestus* in many places (even at the type locality of the former), the holotype and paratypes of it proved all, upon re-examination, to be the same species.

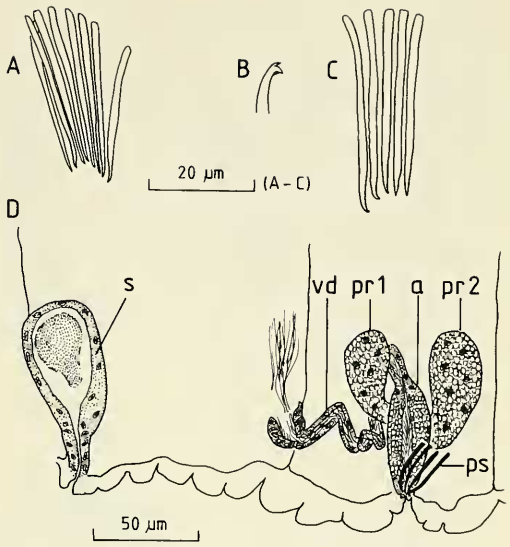


Fig. 1. A, *Phallodrilus rectisetosus*, from Hawaii, penial setae. B–D, *Phallodrilus molestus*, from Hawaii: B, Somatic seta; C, Penial setae; D, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations: a atrium, pr 1 anterior prostate gland, pr 2 posterior prostate gland, ps penial setae, s spermatheca, vd vas deferens.

The key characteristic separating this species from all the others within the complex is the low number of setae; with few exceptions the postclitellar bundles are unisetal. It is otherwise very similar to *P. rectisetosus*, both in terms of number of penial setae and in spermathecal morphology.

Distribution and habitat.—Belize, Barbados (both new records) and Bermuda (Fig. 5); apparently present throughout the Caribbean area. Intertidal and subtidal sand, down to at least about 14 m depth.

Phallodrilus molestus, new species
Figs. 1B–D, 2D–F

Phallodrilus rectisetosus deminutius (part) Erséus, 1979:191–192.—Erséus 1981:table I.

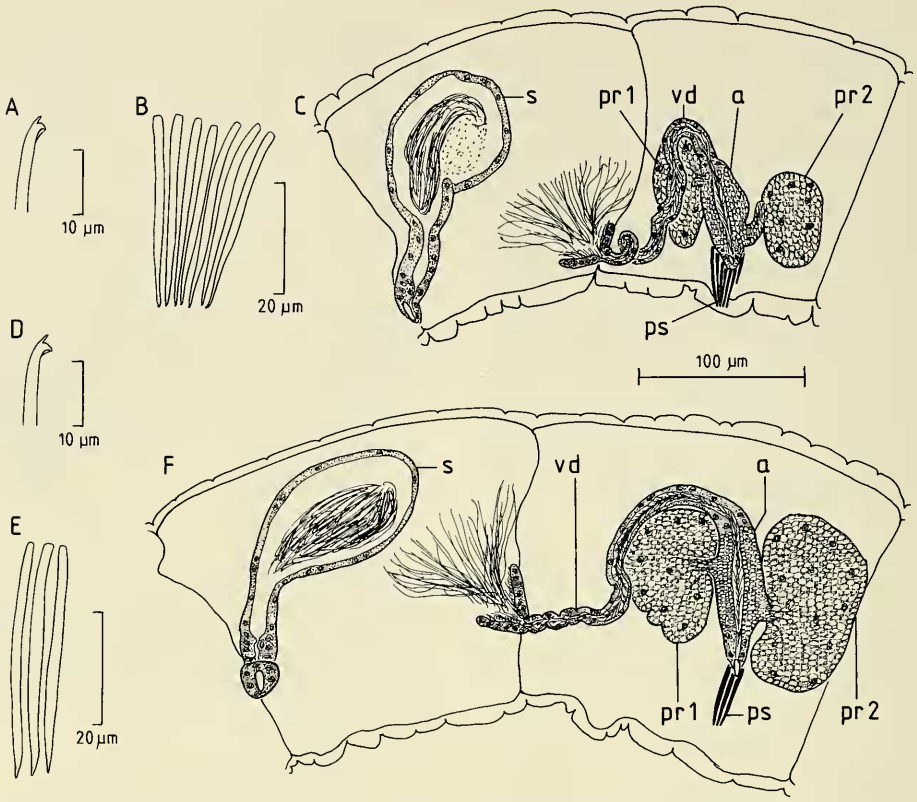


Fig. 2. A–C, *Phallodrilus deminutius,* from Belize: A, Somatic seta; B, Penial setae; C, Lateral view of spermathecae and male genitalia in segments X–XI. D–F, *Phallodrilus molestus,* from Belize: D, Somatic setae; E, Penial setae; F, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations: a atrium, pr 1 anterior prostate gland, pr 2 posterior prostate gland, ps penial setae, s spermatheca, vd vas deferens.

Holotype.—USNM 118352, whole-mounted specimen from outer end of dock at Carrie Bow Cay, Barrier Reef off Belize, 1.5 m, poorly sorted, somewhat muddy, medium to coarse sand (6 Nov 1985).

Paratypes.—USNM 118353–118356, four specimens from type locality.

Other material re-examined (author's collection).—Nine specimens from Bermuda (Erséus 1979:191): two from Ferry Reach (type locality of *P. deminutius*), three from North Rock, one from Tobacco Bay, one from Harrington Sound, and two from Bailey's Bay. One specimen from Fowey Rocks, Miami (Erséus 1979).

Other material.—USNM 118357, one specimen from inner end of bay at river mouth, River Bay, NE Barbados, low water mark, coarse sand (27 Oct 1979).—USNM 118358–118361, four specimens from Paiko Beach, Maunalua Bay, Oahu, Hawaii, barely subtidal mixed sand (2 Apr 1987).—AMS W202443, one specimen from beach at northern side of Palfrey Island, S of Lizard Island, Great Barrier Reef, Australia, lower intertidal, gravel with silt and fine sand (15 Nov 1982).—BMNH 1987.5.1/2, 1987.5.3, two specimens from Mana Island, off Lautoka, Viti Levu, Fiji (5 Dec 1982): one from flat W of Mana Island Resort, subtidal off beach rock, 0.5 m, fine coralline sand with lots of gravel and coral rubble; and one from rocks at W end of North Beach (Mana Island), tide pool in lower intertidal, stones and pebbles with some muddy sand beneath.—Author's collection: 20 speci-

mens from type locality; 177 specimens from 32 other sampling stations in the reef areas near Carrie Bow Cay, Belize (Nov 1985); six specimens from Oahu, Hawaii, four from Paiko Beach (see above), one from off Keehi Lagoon, Honolulu, about 70 m, medium sand (Nov 1986; coll. D. Davis), and 1 from Kawaikui Beach Park, Maunalua Bay (9 Sep 1987; coll. D. Davis).—M. R. Milligan Collection: 1 specimen from about 4 km off mouth of Crystal River, W Florida (Gulf of Mexico), 28°58.7'N, 82°48.7'W, 4 m, coarse sand and shells (Nov 1984; coll. M. R. Milligan).

Etymology.—The species name *molestus* is Latin for "troublesome," referring to the previous difficulties in separating this form from *P. deminutius.*

Diagnosis.—Length 3.0–6.8 mm, 30–43 segments. Bifids almost invariably 2 per bundle, throughout body. Penial setae 28–47 μm long, generally 3–5 per bundle (total range 2–7, $\bar{\chi}$ = 3.1, SD = 0.7, n = 444). Atria 40–80 μm long. Spermathecal ampullae pear-shaped, with sperm in large bundle or mass.

Description of material from Belize (including type material) *and Barbados.*—Length 3.7–5.9 mm, 35–42 segments. Width at XI 0.19–0.24 mm. Bifids (Fig. 2D) 2 per bundle throughout (very occasionally 1 per 'bundle'), 26–42 μm long, 1.5–2.5 μm thick. Penial setae (Figs. 2E, F, ps) 35–46 μm long, about 2 μm thick, generally 3, but sometimes 2, 4 or even 5, per bundle. Male genitalia shown in Fig. 2F. Vas deferens 7–14 μm wide. Atrium 45–80 μm long, 20–30 μm wide. Spermathecae (Fig. 2F, s) 130–210 μm long, consisting of short ducts and pear-shaped, thin-walled ampullae; latter narrower ectally than entally, maximally 25–95 μm wide; sperm as thick bundle or large mass.

Description of material from Hawaii, Great Barrier Reef and Fiji.—Length 3.2–5.2 mm, 36–42 segments. Width at XI 0.20–0.35 mm. Bifids (Fig. 1B) 30–42 μm long, 1.5–2.5 μm thick, 2 (anteriorly sometimes only 1) per bundle throughout. Penial setae (Fig. 1C) 28–42 μm long, 1.5–2 μm thick, generally 4–5 (total range 3–6) per bundle. Male genitalia shown in Fig. 1D. Vas deferens 5–7 μm wide. Atrium 40–60 μm long, 15–23 μm wide. Spermathecae (Fig. 1D, s) 60–90 μm long, consisting of short ducts and pear-shaped, thin-walled ampullae; latter narrower ectally than entally, maximally 28–42 μm wide; sperm as large mass, or absent (lumen then filled with a round mass of secretion, as shown in Fig. 1D).

Variation in number of penial setae per bundle (Fig. 4).—Belize (n = 394): range 2–5, $\bar{\chi}$ = 3.0, SD = 0.6.—Bermuda (n = 18): range 2–5 (one bundle with 7), $\bar{\chi}$ = 4.1, SD = 1.1.—Miami (n = 2): range 4–5, $\bar{\chi}$ = 4.5.—Gulf of Mexico (n = 2): 2 (both bundles).—Barbados (n = 2): 3 (both bundles).—Hawaii (n = 20): range 3–6, $\bar{\chi}$ = 4.4, SD = 0.7.—Great Barrier Reef (n = 2), range 3–4, $\bar{\chi}$ = 3.5.—Fiji (n = 4): range 4–5, $\bar{\chi}$ = 4.3, SD = 0.4.

Remarks.—Some of the specimens from Bermuda and Florida were previously (Erséus 1979) identified as *P. rectisetosus deminutius,* but they have bisetal bundles of bifids throughout the body, and a low number of penial setae, the two features unique for the form now recognized as a separate species, *P. molestus.*

Distribution and habitat.—Belize, Barbados, Florida, Bermuda, Hawaii, Great Barrier Reef, Fiji (Fig. 5). Lower intertidal and subtidal sands, down to at least 70 m depth. *Phallodrilus molestus* is one of the most common tubificids on the Barrier Reef off Belize.

Phallodrilus heronensis Erséus, 1981
Fig. 3

Phallodrilus rectisetosus heronensis Erséus, 1981:15–17, figs. 1–3, table I.

Type material.—In Queensland Museum (G 12544–12551): eight specimens from Heron Island, Great Barrier Reef, Australia (see Erséus 1981).

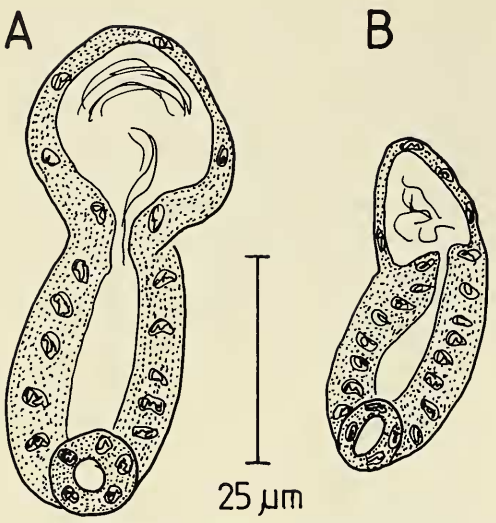


Fig. 3. *Phallodrilus heronensis,* spermathecae: A, Specimen from Fiji; B, Specimen from Aldabra.

New material.—BMNH 1987.5.4/5 and 1987.5.6, one sectioned and two whole-mounted specimens from reef flat off "Picnic Point," Mana Island, off Lautoka, Viti Levu, Fiji, 0.5 m, coarse gravelly sand (7 Dec 1982).—USNM 104129–104131, three specimens from Aldabra Atoll (Seychelles), coll. K. Fauchald: one from Basin Lebine, 0.5 m, from *Caulerpa* sp. clump (13 Mar 1985); and two from in front of laboratory, in *Thalassodendron* (Apr 1983).

Diagnosis.—Length 2.3–4.6 mm, 33–39 segments. Bifids 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae 20–35 µm long, 4–7 (occasionally up to 11) per bundle ($\bar{\chi}$ = 6.4, SD = 1.6, n = 30). Atria very small, only 25–40 µm long. Spermathecae club-shaped, with long ducts and small, somewhat spherical ampullae; latter containing a few loosely arranged spermatozoa.

Description of material from Fiji.—Length, 2.7–2.9 mm, 35–37 segments. Width at XI 0.26–0.27 mm. Bifids 30–35 µm long, 1.5–2 µm thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae about 25–30 µm long, 4–5(6) per bundle. Atrium about 30 µm long, about 10 µm wide. Spermathecae (Fig. 3A) 55–70 µm long, maximally 17–26 µm wide, with sperm as loose bundle in ampullae.

Description of material from Aldabra.—Length 2.3–3.5 mm, 33–37 segments. Width at XI 0.10–0.18 mm. Bifids 25–37 µm long, 1–2 µm thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae 20–25 µm long, 7(9) per bundle. Atrium about 25–30 µm long, 11–15 µm wide. Spermathecae (Fig. 3B) only 40–47 µm long, 10–20 µm wide, with a few spermatozoa in ampullae.

Variation in number of penial setae per bundle (Fig. 4).—Heron Island, Great Barrier Reef (n = 18): range 5–11, $\bar{\chi}$ = 6.7, SD = 1.6.—Fiji (n = 6): range 4–6, $\bar{\chi}$ = 4.8, SD = 0.7.—Aldabra (n = 6): range 7–9, $\bar{x}$ = 7.3, SD = 0.7.

Remarks.—The very small atria and spermathecal ampullae are diagnostic for *P. heronensis,* and separate it from the other species of the complex.

Distribution and habitat.—Aldabra, Fiji (new records) and Great Barrier Reef (Fig. 5). Intertidal and barely subtidal sand, down to at least 0.5 m depth.

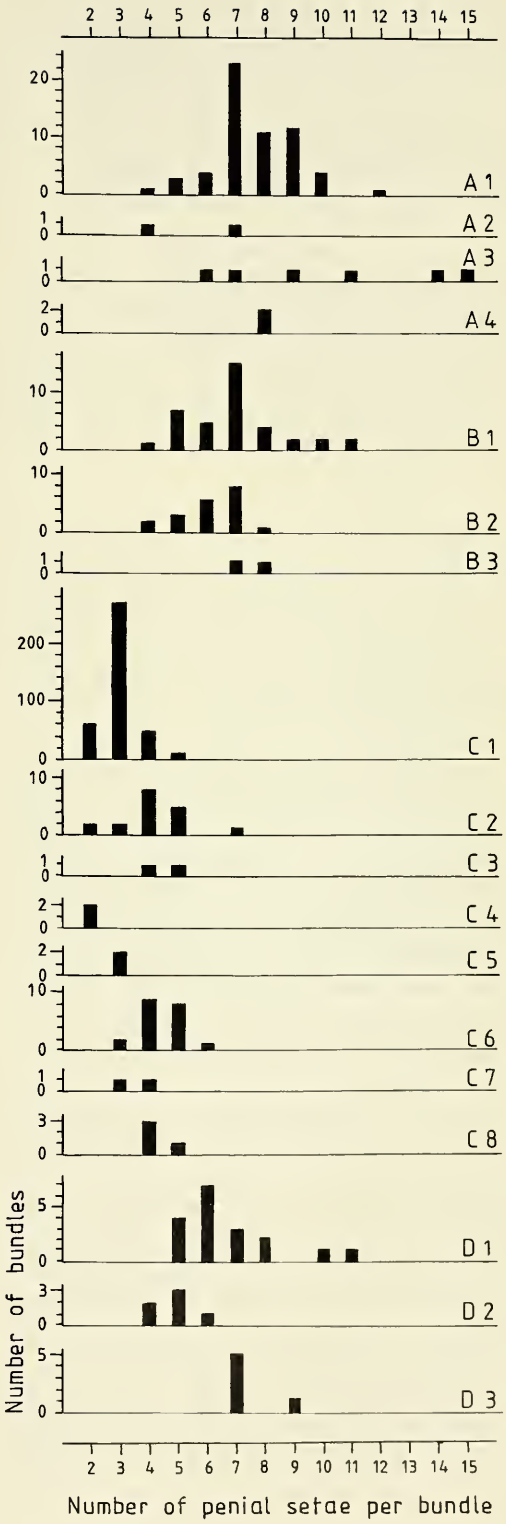
Discussion

The species complex considered here is a homogeneous group of marine tubificids, with a few variable and somewhat confusing characters that made the original classification difficult (Erséus 1979, 1981, 1985). The new specimens from Florida, Belize, Barbados, Hawaii, Fiji, Australia and Aldabra, however, have revealed a pattern in the variation indicating the presence of four distinct species. Three characters have shown to be particularly useful.

First, the bifid (somatic) setae, which morphologically are more or less identical in the four forms (Figs. 1B, 2A, D), are up to 3(4) per bundle anteriorly, diminishing to 2 per bundle posteriorly, in *P. rectisetosus* and *P. heronensis,* whereas the bundles are

(almost invariably) bisetal anteriorly and unisetal posteriorly in *P. deminutius*. Such a posterior decline in setal numbers does not characterize *P. molestus*, which has bisetal bundles throughout the body. Secondly, the latter species is also unique in its very low number of penial setae, in fact it is the only species in the group that in most cases can be separated solely on the basis of this number. The other three species have very wide, overlapping ranges for the numbers of penial setae (see Fig. 4), the means being very close to each other. Thirdly, although variable in shape, the spermathecal ampullae of *P. rectisetosus, P. deminutius* and *P. molestus* are large (relative to those of *P. heronensis*) and pear-shaped, sometimes with a tendency towards a bipartition (cf. Erséus 1979:fig. 6), and they are not always clearly set off from the ducts. In *P. heronensis*, however, the ampullae are very small, roundish and clearly set off from the (relatively long) ducts (Fig. 3).

Some of these differences may appear slight and not, per se, interspecific. For instance, a variation in the number of somatic setae between one and two, or two and three, per bundle may be considered intraspecific in other tubificid species. However, in the present study, which covers material from 13 different areas of the world (Fig. 5), each individual could rather easily be assigned to one of the four distinct forms; no intermediates were found. The forms are not even fully separated geographically, thus refuting the alternative of them being geographical races. As illustrated in Fig. 5, two forms are



→

Fig. 4. Variation in the number of penial setae per bundle, in various populations of the *Phallodrilus rectisetosus* complex. A, *P. rectisetosus* from Italy (A1), France (A2), Saudi Arabia (A3), and Hawaii (A4); B, *P. deminutius* from Bermuda (B1), Belize (B2), and Barbados (B3); C, *P. molestus*, from Belize (C1), Bermuda (C2), Miami (C3), Gulf of Mexico (C4), Barbados (C5), Hawaii (C6), Great Barrier Reef (C7), and Fiji (C8); D, *P. heronensis* from Great Barrier Reef (D1), Fiji (D2), and Aldabra (D3).

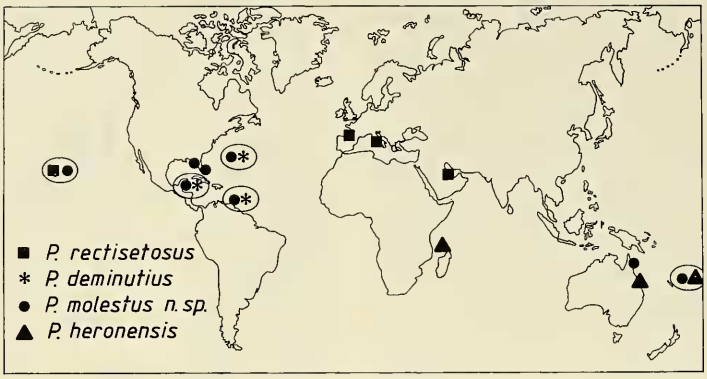


Fig. 5. Geographical distribution of the species within the *Phallodrilus rectisetosus* complex. Records of two species from the same area are encircled.

sympatric (in various combinations) in 5 of the 13 areas studied. The records suggest, however, that the Caribbean *P. deminutius* and the Indo-Pacific *P. heronensis* may be geographically more restricted than the apparently circumtropical *P. rectisetosus* and *P. molestus*.

Although these four species without doubt are closely related, they do not necessarily constitute a strictly monophyletic group. Their simple male ducts and penial setae do not appear to be apomorphic traits, but rather less derived structures possibly similar to those of an ancestral phallodriline; the male genitalia of most other members of the subfamily appear to be derived from the biprostate (i.e., unmodified) atria of *Phallodrilus*. This implies that the *rectisetosus* group, as well as the genus *Phallodrilus* as a whole, is likely to be paraphyletic. The recently described *P. duplex* Erséus, 1987, from the Mediterranean coast of Israel, most probably belongs to the same lineage. It has bisetal bundles throughout body, except for the penial ones which are trisetal, and it thus appears to be very closely related to *P. molestus*; it is distinguished from the latter by its somewhat more slender atria and the modified tips of its penial setae (see Erséus 1987). Particularly the latter feature makes it a slightly more derived species than the four taxa treated in the present paper.

Acknowledgments

I am indebted to Dr. K. Ruetzler (USNM and Carrie Bow Cay field station), Dr. F. Sander (former director, Bellairs Research Institute), and Dr. B. Goldman (former director, Lizard Island Research Station), for working facilities at their respective laboratories; to Dr. L. Zann (Suva) for assistance in planning my work and arranging a research permit in Fiji; to Dr. K. Fauchald (USNM), Drs. H. Spero and M. Gustavson (Barbados), Dr. F. Doujak (Canberra), and Mr. D. Davis (now in San Francisco), for most valuable assistance in the field work; to Dr. R. O. Brinkhurst (Sidney, Canada), Mr. M. R. Milligan (Sarasota, FL), and Dr. K. Fauchald, for making material in their collections available for study; to Ms. B. Löfnertz and Mrs. A. Falck-Wahlström (Göteborg) for skillful technical assistance; to the Smithsonian's Walter Rathbone Bacon Scholarship Fund, and the Swedish Natural Science Research Council, for financial support; and to R. O. Brinkhurst for critical review of the manuscript. This paper is contribution number 244 of the Smith-

sonian Institution's Caribbean Coral Reef Ecosystems Program. It is also a contribution from the Bellairs Research Institute of McGill University, Barbados.

Literature Cited

Erséus, C. 1979. Taxonomic revision of the marine genus *Phallodrilus* Pierantoni (Oligochaeta, Tubificidae), with descriptions of thirteen new species.—Zoologica Scripta 8:187–208.

———. 1981. Taxonomic studies of Phallodrilinae (Oligochaeta, Tubificidae) from the Great Barrier Reef and the Comoro Islands with descriptions of ten new species and one new genus.—Zoologica Scripta 10:15–31.

———. 1985. Annelida of Saudi Arabia. Marine Tubificidae (Oligochaeta) of the Arabian Gulf Coast of Saudi Arabia.—Fauna of Saudi Arabia 6(1984):130–154.

———. 1987. A new species of *Phallodrilus* and records of two other marine Tubificidae (Oligochaeta) from the Mediterranean coast of Israel.—Israel Journal of Zoology 33(1984/85):73–78.

Zoo-tax, Swedish Museum of Natural History, Stockholm, and (postal address:) Department of Zoology, University of Göteborg, Box 25059, S-400 31 Göteborg, Sweden.